OBSERVATIONS ON THE ECOLOGY OF EUPLOEA CORE CORINNA (NYMPHALIDAE) WITH SPECIAL REFERENCE TO AN OVERWINTERING POPULATION

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ABSTRACT. A study of a sub-tropical overwintering aggregation of the common crow butterfly, *Euploea core corinna* (Nymphalidae: Danainae), has been made on the campus of Griffith University, Brisbane, Australia. Observations on the temporal and spatial phenology of the aggregation, together with the sex ratio, reproductive status, individual fat content and physical condition of butterflies within the aggregation are presented. The aggregation was restricted to the upper reaches of a gully on the campus between mid-May and late July. Physical conditions in the gully (temperature, humidity and wind) were less severe than in adjacent areas. The butterflies in the gully were reproductively inactive. We suggest that such aggregations, apart from avoiding severe winter conditions, may also serve as mating concourses at the end of the winter season.

The common crow butterfly, *Euploea core* (Cramer), is widely distributed in the Indo-Australian region and is represented in Australia by the subspecies, *corinna* (W. S. Macleay) (Fig. 1). Recent general accounts of its life history are given by McCubbin (1971) and Common & Waterhouse (1972). These authors summarize information on foodplants, phenology, behavior and morphology, principally collated from the observations of field naturalists. McCubbin (1971) alluded to the formation of overwintering aggregations of this species in sheltered coastal sites and offshore islands in the tropics and subtropics of northern and eastern Australia.

Winter aggregations are also recorded for a variety of Australian danaines including *E. sylvester* (F) and *E. tulliolus* (F), *D. hamatus* (W. S. Macleay) and *D. affinis* (F). They are restricted to the period May–September, the dry season (Leeper, 1970) in north-eastern Australia, when temperatures remain above freezing for the most part (but see the discussion below).

The discovery of an aggregation of *Euploea core corinna* on the campus of Griffith University, Brisbane, Queensland in May 1979, prompted our observations on the population biology of the butterfly. These observations were continued from May to September although the aggregation had largely dispersed by early July. The results of these studies are presented in the present paper. In addition, we have taken the opportunity to speculate on the role and evolution of over-wintering behavior of this type.

Our observations included estimates of the size of the overwinter-

ing population, its sex ratio, physical condition and the fat content of samples of individuals. The reproductive status of female butterflies was also examined. These studies, together with environmental measurements and behavioral observations provide a systematic basis for further research.

MATERIALS AND METHODS

The Study Area

The overwintering aggregation was centered in a gully which forms the upper section of the Rocky Waterholes Creek catchment adjacent to the Griffith University forest study area (27°33'E, 153°05'S) some 10 km S of Brisbane, Queensland. A general description of the area is given by Birk (1979). The topography of the site is shown in Fig. 3. The vegetation comprised relatively open mixed eucalypt forest with an overstory dominated by Angophora woodsiana F. M. Bailey, Casuarina littoralis Salisb., Eucalyptus baileyana F. Muell. and E. umbra R. T. Bak (Fig. 2). There were also many standing dead trees, notably Casuarina, in the area, especially along the lower sides of the gully. The understory comprised a variety of woody shrubs including Pultenaea villosa Willd., Alphitona excelsa (Fenzl.) Benth., Acacia cunninghami Hook., A. aulocarpa A. Cunn. ex Benth. and Xanthorrhoea johnsonii R. Br. A sparse and varied herb layer of grasses and forbs was present.

The approximate boundaries of the overwintering aggregation are indicated on the map (Fig. 3). Essentially, the overwintering insects occurred along the floor and lower sides of the gully, concentrating in the upper, deeper area to the north. The lower end of the concentration was ill-defined and one or two insects could be stirred up along much of the length of the gully floor throughout the period of observation.

Environmental Monitoring

During much of the study, continuous records of shade temperatures and relative humidity were collected at two locations within the study area. These are indicated in Fig. 3 and were chosen to permit microclimatic characterization of the overwintering site itself and the adjacent forest. These observations were made using two thermohydrographs maintained in screened boxes at ground level. A maximum and minimum thermometer accompanying each instrument permitted weekly calibration of the records of temperature. Information on prevailing wind directions was collected from records for Brisbane city made available by the Bureau of Meteorology.



FIG. 1. Adult of *Euploea core*. FIG. 2. General view of overwintering site.

Population Parameters

The population of butterflies was sampled on eight occasions from 4 June to 11 July 1979 with an additional post-winter sample taken in September. On each occasion two collectors spent 15–20 min netting adults which were temporarily caged in darkened boxes. They were subsequently tagged using the method of Urquhart (1960), em-

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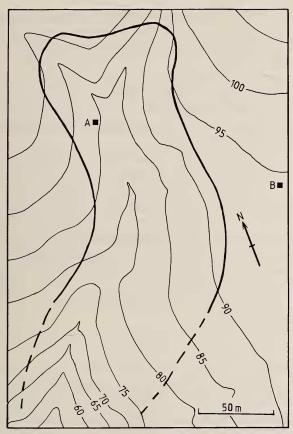


FIG. 3. Contour map of the upper catchment of Rocky Water Holes Creek, Brisbane, Queensland indicating the meteorological monitoring sites (A and B) and the approximate boundaries of the overwintering colony of *Euploea core corinna* (indicated by the heavy line).

ploying self-adhesive, individually numbered labels. These were affixed to the forewings of the insects by folding them over the costal margin after rubbing the scales off this region of the wing. Sex and wing condition of the captured butterflies were noted. A three point scale was adopted to categorize wing condition, *viz*, "intact" (perfect wing-margins), "chipped" (up to approximately 20 mm² of wing missing), and "very chipped" (more than 20 mm² of wing missing).

A subsample of males and females was removed for determination of fat content (see below) and the females were dissected to check whether they had mated (indicated by the presence or absence of spermatophores in the bursae copulatrices) and amount of ovarian development, if any.

The frequencies of recapture of marked insects in the first six sam-

ples were used to estimate the size of the colony by calculation of simple Lincoln indices. In addition, preliminary estimates of survivorship were obtained from the recapture data using the approach of Ehrlich & Gilbert (1973).

Fat Content

The subsamples of butterflies were returned, live, to the laboratory within 20 min of capture. They were killed and frozen immediately for later analysis (stored at -12° C).

In general, we used the technique of Tuskes & Brower (1978) to determine total fat content of the insects. The insects were first dried for 48 h at 50°C. They were weighed using a Mettler HR4AR balance and ground to a powder using a glass pestle and mortar. Using the method of Tuskes & Brower (1978), the powder was weighed and transferred to a glass vial to which was added 15 ml of a 2:1 chloroform/methanol mixture. The vials were sealed and agitated gently for 24 h. The solvent mixture was subsequently filtered off and evaporated to dryness in a preweighed glass tube. The reweighing of the tube, this time with the dry residue, permitted estimation of the gross lipid content for each insect.

Other Observations

On each sampling occasion we made notes on the behavior of the butterflies. In addition, we recorded occurrence of other species of butterflies and flowering plants available as nectar sources.

A sequence of oviposition observations by this species on plants of Asclepias fruticosa (L.) in an experimental plot 1.0 km from the overwintering site, was available from a long term population study of Danaus plexippus L. This provided a useful adjunct to the overwintering study, as did casual observations on the presence or absence of E. c. corinna adults elsewhere on the campus and adjacent areas.

RESULTS

Environmental Monitoring

Table 1 summarizes the temperature and relative humidity readings taken in the gully and on the adjacent ridge from 15 June to 16 July 1979. These indicate that the gully provides a buffered environment relative to that of the adjacent ridge. Minimum temperature readings are consistently at least 2°C higher in the gully than on the ridge. The regression of ridge minimum temperatures on corresponding readings from the gully indicates that the differences between gully and ridge minima decrease as (gully) temperatures increase. Maximum daily temperature readings are slightly lower in the gully, but are not significantly different from the ridge readings.

Relative humidity readings are consistently higher in the gully relative to the ridge both during the day and night. During the day the gully is a constant 5% more humid than the ridge over the range of readings (slope ≈ 1.0 , intercept ≈ 5). At night the differences are smaller as overall humidity increases (slope > 1.0).

The gully is also sheltered by its N–S orientation from the influence of prevailing winds. Between May and August these are W to S–W in the mornings and S–E to N–E in the afternoons.

Population Parameters

Table 2 contains the results of the population studies and estimates of population parameters derived from them.

The estimates of density (x) and the associated standard deviations (s) given in columns 4 and 5 of the Table are derived by calculation of a simple Lincoln index on subsequent pairs of observation using the formulae:

and

$$x = \frac{an}{n}$$
$$s^{2} = \frac{a^{2}n(n-r)}{r^{3}}$$

where n is the total number of individuals in the second sample, a is the total number of marked individuals and r is the total number of recaptures (see Southwood, 1966, for further discussion of the method, its assumptions and drawbacks). The very small number of recaptures and consequent large variances demand that we discount the estimates for 7 and 27 June. The intervening figures, however, we feel reflect the actual size of the aggregation within the stated limits. In summary, there were 1200–1600 individuals in the aggregation during the winter period of study.

Throughout the study there was a preponderance of males (column 6 of Table 2) in our samples. The temporal variations in the sex ratio we ascribe to sampling error and suggest that the overall mean of our estimates of the ratio (2.16, s = 0.606) is the best estimate for the overwintering period as a whole. The sex-ratio in the spring sample was higher than most of the winter estimates but, again, this may be due to sampling error.

The condition of the butterflies using the criteria outlined above, is summarized in columns 7, 8 and 9 of Table 1. Throughout June, the condition of insects sampled was good with more than 90% of

") and an adjacent area	
ative humidity data collecting in the overwintering site ("gully")	rentheses.
TABLE 1. Summary of temperature and rel	'ridge"). Standard deviations are given in pa

Datum	No. of observations	Gully	Ridge	Regression of ridge (R) on gully (G)	R value
Mean minimum temp. (°C)	27	9.6 (2.67)*	7.9(2.87)*	$R_{min} = 1.06G_{min} - 2.31$	0.9862
Mean maximum temp. (°C)	28	$21.4(1.73)^{NS}$	$21.8(1.88)^{NS}$	$R_{max} = 0.85G_{max} + 3.71$	0.7935
Temp. range (°C)	1	7-24	5-25	1	Ι
Mean night RH (%)	26	89.5 (2.5)**	$82.8(4.2)^{**}$	$R_{nig} = 1.43G_{nig} - 45.0$	0.8293
Mean day RH (%)	28	51.0(11.1)*	44.0~(11.2)*	$R_{day} = 0.98G_{day} - 4.96$	0.9583
RH range	I	34–98	27-90	1	1
**, *, NS: Indicates level of significance of difference ($P < 0.001$; $P < 0.05$, not significant).	ce of difference (P <	0.001; P < 0.05, not signifi	icant).		

TABLE 2. Population parameters of the subject population of Euploea core corinna. KEY: x indicates a mean estimate, s, its standard deviation and n the number of observations. See text for further explanation.

	Totol	No of	Lincoln Inde: estimate	ı Index nate	males	Cor	Condition (%) ¹		Females		Fa	Fat content (%)	
Sampling dates (1979)	captured	marks	x	s	females	Ι	С	VC	(%)	Development	x	s	u
Winter													
4 June	48	I	I	Ι	1.29	27	71	61	0	None	24.3	3.46	7
7 June	47	Γ	2256	2232	3.27	36	59	ы	0	None	I	I	I
12 June	47	4	1116	534	2.13	30	68	01	0	None	I	I	I
15 June	99	9	1562	608	1.87	27	69	4	0	None	21.0	3.86	11
22 June	37	ы	1539	640	2.70	30	65	ы	0	None	I	I	I
27 June	37	61	4532	3117	2.27	15	84	1	0	None	I	I	1
6 July	9	1	I	I	2.00	00	52	ر ۱۹	0	None	1	I	Ι
11 July	11	I	I	I	1.75 §	67	3	- 01	0	None	17.9	3.25	11
Spring													
9–15 September, 1979	17	ł	I	I	3.25	46	29	25	100	Advanced	18.3	2.96	4
¹ I = "intact"; C = "chipp	ed"; VC = "	very chippe	ed."										

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captures in "intact" or "chipped" condition. The proportion of "very chipped" individuals rose sharply in the final winter sample (11 July) and showed a further increase in the spring sample.

The samples of females dissected during the winter period were all non-mated with no apparent ovarian development. This was in sharp contrast to the spring sample, in which all females examined were mated and had recognizable ova in their ovarioles.

The "longevity" of adult butterflies in the gully can be estimated from known minimum ages of recaptured insects. Table 3 summarizes this information and is based on animals marked between 4 and 27 June. The number of recaptures, 22 out of 282 released, is low and makes the survivorship estimates at best a first approximation. These life-span estimates are better considered as residence times in the marked population and as such are compounded of daily mortality and movements up and down the gully. Males have a longer mean "life-span" in the gully relative to that of the females (11.2 vs. 7.9 days). These differences are not due to sampling bias as the proportion of male to female recaptures (13:7) is similar to our estimates for the overall population (2:1). Neither is the difference due to differences in mortality, as the following four individuals indicate. Female number 50 was marked on 7 June and recaptured on 7 September in the gully. This individual was in "chipped" condition when first marked and had, presumably, been alive for some time before being marked. She was "very chipped" when recaptured. Female 96 was marked on 12 June in "intact" condition and was recaptured on 3 September outside the gully area (760 m to the E) in "chipped" condition. Male number 293 was intact when marked on 14 September and "chipped" when recaptured 980 m E of the gully on 11 October. Male number 91 was marked on 12 June and recaptured 122 days later, 3 km SSE of the campus. All of these butterflies had further expectation of life if wing condition is taken as an indicator of age. This is particularly true of female 96, which on dissection revealed early egg development and, presumably, would have had the bulk of her reproductive life ahead of her. E. core is therefore capable of living as long as 160 days if we take 80 days as a conservative estimate of the mean life expectancy (females 50 and 96 lived an average of 87 days at least). The difference in male/female residence times in the gully can be attributed to differences in vagility; females being more likely to move up and down the gully than males, and hence less prone to recapture in the limited netting area.

Fat Content

Results from analyses for total fat content are presented in columns 12–14 of Table 2. They indicate a steady and significant decline in

Minimum no. of days surviving	Males	Females	Total
3	_	2	2
5	1	1	2
7	2	_	2
8	3	1	4
10	3	1	4
11	1	1	2
15	1	1	2
20	1	_	1
26	1	—	1
Total	13	7	20
Mean minimum life-span (MMLS) ¹	11.2	7.9	10.0
% daily survival (S) ²	91.1	87.3	90.0

TABLE 3. Longevity of marked *Euploea core corinna* in the overwintering aggregation. (See text for further comment.)

 1 MMLS = Σ min days survived \times number surviving/Total number recaptured (Ehrlich & Gilbert, 1973). 2 S = 1/1 - MMLS (Edmunds, 1969).

the fat content of the overwintering butterflies from 24.3% on 4 June to 17.9% on 11 July. Results for males and females did not differ significantly and, hence, the estimates given combine figures for both sexes. The fat content of the spring sample showed an increase over that of the last winter sample although this was not significant, and was probably due to the small sample size of the spring insects.

Other Observations

During the overwintering period a number of persistent behavior patterns were observed in the adult insects. Most insects spend the greater proportion of their time at rest on the vegetation at levels from about 1 m to 6 m from the ground. They were particularly numerous on the branches of standing dead *Casuarina* trees. When undisturbed and during sunny periods several desultory flights of a few meters could be observed at any time. When disturbed, however, large numbers of insects would fly up and down the gully at about head height. No substantial lateral movements were observed. Such flights were frequently in apparently coordinated groups with up to a dozen or more insects moving in unison. These drifts were of both sexes, but were not mating flights and no mating behavior was seen in the period of overwintering. This correlates with the unmated status of dissected females (see above).

Very few other butterflies were observed in the gully at the same time as *E. core*, although several *Danaus chrysippus petilia* were seen, apparently passing through the area. A few resident *Melanitis leda* (Satyrinae) were present in the gully but their characteristic low

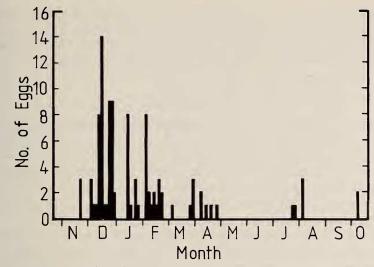


FIG. 4. Histogram of numbers of eggs of *Euploea core corinna* laid on Asclepias plants from November 1977 to October 1978.

vagility and ground dwelling habit excluded any but the most minor interaction with *E. core*.

During the overwintering period the only obvious nectar sources in the gully were a few flowers of the weed Ageratum houstonianum Mill. At the end of the period of observation, however, when the aggregation was dispersing, a variety of species were in flower including Gomophlobium latifolium Sm., Leptospermum flavescens Sm., and Xanthorrhoea johnsonii, on all of which E. core was observed to feed. Many other herbs and shrubs also begin to flower in the sclerophyll forest at this season.

A comparable period of overwintering was also defined, albeit circumstantially, in the observations on oviposition phenology of *E. core* made in a prepared plot of *Asclepias* spp. These results are for the previous winter (November 1977 to October 1978) and are presented as Fig. 4. Not only do these data support our observations concerning the temporal and spatial integrity of the overwintering aggregation, they are also the first records of the phenology of egg-laying in the species. The spatial integrity of the aggregation was evidenced largely by the total absence of sightings of the butterfly in areas adjacent to the gully in the period, early June to early July 1979. Subsequently butterflies, several of which bore our labels, were observed regularly in areas of the campus away from the gully. One such insect was retrieved in September, 3 km from the site of the gully. After the breakup of the overwintering aggregation, mating and ovipositing activity began, although insects remained in the gully. Oviposition on campus took place on leaves of the vine, *Parsonsia straminea*, on which larvae were subsequently reared successfully.

DISCUSSION

In any consideration of overwintering in adult butterflies, the reference point must be the extensive work on the phenomenon in North American *Danaus plexippus*. Key classical and recent works on the species in this context include Urquhart (1960, 1965), Urquhart & Urquhart (1976), Brower et al. (1977), Tuskes & Brower (1978) and Calvert et al. (1979). In Australia such aggregations of *D. plexippus* have been reported, briefly, by Smithers (1965).

Euploea core in Australia, unlike D. plexippus in North America, is not migratory although it does show occasional extensions in range southwards in favorable seasons (see, for example, Kitching et al., 1978). The existence of overwintering aggregations in parts of its range, then, represent contractions in its distribution in response to unfavorable seasonal conditions and not the end-points of some regular directional mass movement. Such contractions of range are recorded for D. plexippus in Australia by Smithers (1977) although these result in restricted winter breeding areas. They also occur on a continental scale whereas E. core appears to be concentrated in, at most, a regional scale. The overwintering swarms of D. plexippus that have been observed in Australia are not, as far as is known, associated with any regular migrations and occur in early winter adjacent to breeding ranges (Smithers, 1965).

That the aggregations observed in *E. core* are in areas of more equable climate than elsewhere in their environs is evidenced by the climatic data presented in this paper. The few degrees amelioration in minimum temperatures experienced in the gully would be sufficient to permit its inhabitants to avoid the occasional light frosts occurring during most winters in this subtropical region. In addition, the region is one of summer rainfall with little or no fresh vegetation growth during the period when the overwintering aggregations occur. The clustering behavior, thus, can be regarded partly as a further response to the lack of food, both for larvae and imagines, which Wolda (1978) uses to account for the marked seasonality he observed in various neotropical phytophagous insects.

We suggest that the butterflies are in a largely quiescent stage during the period of aggregation and evidence for this is derived from closer examination of the data on fat content. Following Gibo & Pallett (1979) it is possible to use the metabolic data of Zebe (1954) to examine the energetic demands of butterflies in terms of their wet weights. These authors suggest a basal metabolic rate for butterflies (based initially on data from Vanessa sp.) of 2 cal/g/h. If we calculate the energetic demands of butterflies of the mean wet weight of our samples of *E. core* between 4 and 15 June we arrive at a figure of 99.8 cal or, taking the caloric equivalent of fat to be 9.09 cal/mg (Weiss-Fogh, 1970), an equivalent weight of 11.0 mg of fat. This compares favorably with our estimate of the loss of fat over that period (12.1 mg) suggesting for this period that the insects were indeed quiescent, living off their reserves of fat. A similar calculation for the period 15 June to 11 July produces an expected fat loss of 31 mg which is considerably more than the observed 12.2 mg decline. This suggests that some food intake occurred during this latter period and, indeed, the observed coincidence of the time of breakup with the appearance of a variety of floral nectar sources lends support to the idea that nectar feeding begins at and, indeed, may trigger the end of the overwintering aggregation.

Calvert et al. (1979) report considerable predation on clustered D. plexippus by birds, notably orioles and grosbeaks. Evidence of predation on *E. core* was rare. One individual with an obvious beak mark was taken and a few wings were found on the gully floor, possibly evidence of spider predation. Of the local birds the pied butcher bird, Cracticus nigrogularis Gould, a generalist predator, was noted in the gully and is a likely candidate as predator of the butterflies. Bowers & Wiernasz (1979) have defined particular types of wing damage in the satyrine, Cercyonis pegala, which they attribute to avian predation. Their categories include triangular tears, straight tears across major veins and symmetrical damage to opposite or ipsilateral wings. Although we noted the extent of wing-chipping in *E. core* throughout the period of study, damage of the type indicated by these authors was not observed and such wing-tearing as was noted seems much more likely to be the result of contact with vegetation and other physical wear and tear than of encounters with predators. We conclude that in the period for which we have data predation was not high.

From an evolutionary point of view the question, "why form overwintering aggregations?" is of interest. Butterflies may overwinter in any one of their life history stages and, even in the same region, different groups exhibit different strategies. That the danaines are so apt to exhibit what is perhaps the least common road, and overwinter as adults, frequently in aggregations such as that described here for *E. core* requires some further consideration. Tuskes & Brower (1978) observed that during the latter part of overwintering aggregations of D. plexippus, mass mating flights occur. Although no mating was observed in our studies, the high proportion (100%) of mated females in our September sample and the higher proportion of "very chipped" insects in our later samples provides, in our view, strong circumstantial evidence that mating in this species is coincident with the period of breakup of the overwintering aggregation. This, with Tuskes & Browers' (1978) observations, leads to the suggestion that such aggregations may serve as mating concourses, adding to the variety of the mechanisms described by Shields (1967) and Scott (1968, 1974), among others, by which butterflies overcome the mate-finding problem so acute in animals with widely dispersed oviposition sites.

The observations presented here leave a number of fascinating questions unanswered. Foremost among these are matters pertaining to the mode of formation of overwintering groups such as the one described here. Do late summer emergents actively seek out an overwintering site or are they "captured" by the site, as it were, when passing through? Given the propensity for these and other butterflies to use gullies as natural flyways, the latter mechanism seems most likely. This then raises questions about the role of such sites in the dynamics of the local population. To what extent are such sites "traditional"? Even allowing for the exceptional longevity of the species. the individuals which enter the overwintering site will be at least one generation removed from those that dispersed from such sites the previous spring. How many sites are there in a given area and how does this relate to the movement potential of the species? These and other questions must await results of further investigation now in progress.

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